

PERVASIVE HYDROLOGIC EFFECTS ON FRESHWATER MUSSELS AND RIPARIAN TREES IN SOUTHEASTERN FLOODPLAIN ECOSYSTEMS

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Abstract: We present long-term growth trends for 13 freshwater mussel species from two unregulated rivers and one regulated river in the southeastern U.S. Coastal Plain. We also collected baldcypress (*Taxodium distichum* (L.) Rich.) tree cores adjacent to mussel collection sites in one river and directly compared tree and mussel chronologies in this river. To extend our analysis spatially, we examined published baldcypress chronologies from six other unregulated rivers throughout the region. Biochronologies were developed using standard dendrochronology techniques and we explored relationships between annual growth and a suite of streamflow variables in each river. Growth of mussels in unregulated rivers was negatively correlated with annual flood pulse count and May and June discharge, but positively correlated with annual low pulse count and annual number of hydrographic reversals. Baldcypress growth in unregulated rivers was positively correlated with May and June discharge and negatively correlated with annual low pulse count. Mussel growth in the regulated river was not correlated with any streamflow variable suggesting that biological rhythms are decoupled from hydrologic variations in this system. This study shows how interannual variability in streamflow can benefit diverse taxa in floodplain rivers over long periods and how river regulation can disrupt these relationships.

Key Words: dams, dendrochronology, flood pulse, fragmentation, sclerochronology, tree ring

INTRODUCTION

Floodplain rivers of the southeastern United States are highly diverse yet endangered ecosystems (Lydeard and Mayden 1995, Pringle et al. 2000, Ward et al. 2005). Hydrology is a fundamental driver of the structure and function of these ecosystems (Benke et al. 2000, Pringle et al. 2000, Rypel et al. 2008a) and hydrologic alteration by dams has resulted in widespread degradation of ecosystem integrity (Benke 1990, Pringle et al. 2000, Rypel et al. 2006). The importance of flood pulses and resulting inputs of terrestrially derived carbon to aquatic communities is well established (Junk et al. 1989, Benke et al. 2000, Galat and Zweimuller 2001). Nevertheless, because ecological research rarely spans the aquatic terrestrial boundary, little work has compared how neighboring terrestrial and aquatic organisms respond to hydrologic variability (but see LeBreton and Beamish 2000). Empirical data are needed on how hydrology affects diverse organisms in floodplain rivers over long time periods to better evaluate the influence of anthropogenic activity and long-term climatic cycles on these ecosystems.

Biochronologies (time-series estimates of growth inferred from widths of rings in anatomical growth structures) offer a valuable tool to evaluate the response of organisms to variation in environmental conditions over long time periods. Tree rings have long been used to infer past environmental conditions in terrestrial landscapes including occurrence of disturbances such as fire and drought (Fritts 1966, Payette et al. 1990, Speer et al. 2001, Black and Abrams 2005, Girardin et al. 2006, Pettit and Naiman 2007). The emerging field of sclerochronology has applied tree ring techniques to the study of long-term growth variation in aquatic organisms including freshwater fishes (LeBreton et al. 1999, Black et al. 2005) and marine and freshwater bivalves (Schöne 2003, Schöne et al. 2004, Helama et al. 2006, Rypel et al. 2008). Recent confirmation of annual shell ring production by long lived freshwater mussels in the southeastern U.S. (Haag and Commens-Carson 2008, Rypel et al. 2008b) makes available long-term records of environmental variation in these riverine ecosystems.

In this study we explore how growth of freshwater mussels and riparian trees in southeastern floodplain

ivers is shaped by hydrological variation over long periods. We studied growth of 13 mussel species based on validated annual shell rings, from two unregulated rivers and one regulated river, and growth of baldcypress trees based on increment cores, from seven unregulated rivers. We compare growth within and among these species with regard to a suite of hydrological variables identified as important elements of river flow regimes.

METHODS

Freshwater Mussel Growth

We collected mussels from two sites in the Sipsey River, Pickens/Greene Counties, Alabama (33°07'16"N, 87°55'08"W and 33°05'16"N, and at 87°57'27"W), one site in the St. Francis River, Cross County, Arkansas (35°16'12"N, 90°34'58"W), and one site in the Little Tallahatchie River, Panola County, Mississippi (34°23'56"N, 89°47'33"W). The Sipsey is unregulated and unmodified and the watershed is mostly forested; consequently, water quality is high and the river supports one of the most intact aquatic communities in the region (McCullagh et al. 2002). The St. Francis River is largely unregulated in the vicinity of our study site and also supports a diverse mussel fauna. However, much of the watershed is affected by channelization and water diversion projects; land use in the watershed is dominated by large scale, intensive agriculture and the river receives heavy runoff from these activities (Ahlstedt and Jenkinson 1991). The Little Tallahatchie River site is regulated and impounded; our site was located in the tailrace below a major storage reservoir (Sardis Reservoir) and is impounded by a lowhead dam 2–3 km downstream of the site (see Haag and Warren 2007).

We collected a total of 13 mussel species (total shells examined = 203), including representatives of most common species at the sites. The assumption of annual shell ring production has been validated for all of our study species (Haag and Commens-Carson 2008, Rypel et al. 2008). We collected most species alive using SCUBA or by wading, returned animals to the laboratory in coolers, and later dissected tissues from the shells. We collected only freshly dead shells of *Pleurobema decisum* because this species is listed as Endangered under the U.S. Endangered Species Act.

Radial thin-sections (~ 300 µm thick) were prepared from one valve of each specimen using a low speed saw with a diamond impregnated blade (Buehler Ltd., Lake Bluff, IL). Our thin-section methods are described in detail in Haag and

Commens-Carson (2008) and are based on standard methods for bivalves (Clark 1980, Neves and Moyer 1988, Veinott and Cornett 1996). All thin-sections were interpreted independently by two experienced observers using a binocular microscope. We identified annual rings and differentiated them from non-annual shell rings (e.g., disturbance rings) following criteria described by Haag and Commens-Carson (2008). We measured annual growth increments using a binocular microscope and digital camera interfaced with video imaging software. Growth increments were defined as the linear dorsoventral distance (nearest 0.1 mm) between adjacent annual rings at the interface between the prismatic and nacreous shell layers. Increments measured linearly may slightly underestimate growth relative to curvilinear measurements made along the shell surface but the degree of curvature between increments is small and the difference between these two measurements is negligible (Rypel et al. 2008b). For each specimen, we initiated measurements at the most recent complete growth increment (i.e., the year prior to collection) and worked backward in time, allowing us to associate a specific calendar year with each growth increment. The accuracy of our interpretations was evaluated by crossdating each specimen both visually (Yamaguchi 1991) and statistically using the dendrochronology program COFECHA (Rypel et al. 2008b).

After crossdating, we transformed corrected, raw growth increment data into growth indices using the dendrochronology program ARSTAN (Cook and Holmes 1984). ARSTAN removes age related variation in growth due to ontogeny using one of several available detrending functions. To retain as much of the climate signal as possible, we detrended the time series for each individual using a simple negative exponential curve (Fritts 1966, Fritts 1971). The actual increment value was then divided by the value predicted from the curve to generate a unitless index of growth centered on a value of 1 (values > 1 imply above average annual growth, values < 1 imply below average annual growth). The detrended time series for all individuals of a species at a site were then averaged to generate a master chronology for each mussel species in each river.

Tree Growth

We focused on baldcypress trees because they are a long lived and characteristic species of southeastern floodplain forests and are sensitive to climatic and hydrological variation (Stahle et al. 1985, Young et al. 1993, Latimer et al. 1996, Keeland and Young 1997, Hesse et al. 1998, Keeland and

Conner 1999). We collected baldcypress samples from the Sipsey River near the vicinity of the mussel collection sites. We sampled trees adjacent to the main channel in floodplain lakes that are disconnected from the main channel during an average summer but connected during an average winter. We extracted cores from 23 trees using a 53 cm increment borer (Haglöf Inc., Sweden) and placed cores in individually labeled soda straws for transport and storage. Cores were mounted on boards, cross-sectioned with a belt sander, and polished using a series of progressively finer grained sandpapers. We captured digital images of sectioned cores using a high resolution flatbed scanner (Canon CanoScan LiDE 60, Lake Success, New York). Annual growth increments were measured digitally with the dendrochronology image analysis program CooRecorder (Saltsjobaden, Sweden). We used the same crossdating techniques used for mussels to crossdate baldcypress samples. A master baldcypress growth chronology for the Sipsey River was developed in ARSTAN as described above for mussels, including the use of a negative exponential function to detrend each tree measurement time series.

We expanded on our Sipsey River baldcypress chronology by also examining published baldcypress chronologies from six other, largely unregulated rivers in the Coastal Plain physiographic province of the southeastern U.S (Table 1). Tree ring chronologies were obtained from the International Tree ring Database (ITRDB) and were based on sampling and measurement methods similar to ours. We used COFECHA to obtain mean interseries correlations for published baldcypress chronologies. Mean interseries correlations represent the mean correlation (at a site) between each individual chronology and the master chronology for all individuals with that individual excluded; these correlations reflect the strength of the climate-growth relationship for a given population. We used ARSTAN to develop master chronologies for each river following methods described above for mussel and baldcypress samples, and used a Mann-Whitney test to compare mean interseries correlations between all mussel and tree populations.

Correlations with Hydrological Variables

We obtained historical streamflow data for each river from either the U.S Army Corps of Engineers (Sardis Lake Field Office, Sardis, MS; Little Tallahatchie River) or the U.S. Geological Survey (USGS, <http://waterdata.usgs.gov/usa/nwis/rt>; all other rivers). For all sites, we used the closest

available streamflow gage; in all cases the gage was located < 30 river km from our study site. Daily streamflow data for each site were uploaded into the program Indicators of Hydrologic Alteration® (IHA V.7, The Nature Conservancy, Arlington, VA, USA). This program calculates 34 metrics that describe the historical and annual natural flow regime of each river (Poff *et al.* 1997). Because many of these indices are redundant and highly autocorrelated, we selected nine variables (Table 2) that represented each major component of the natural flow regime (Table 2, Olden and Poff 2003). We used Pearson product moment correlations ($\alpha < 0.05$) to examine relationships between mussel and tree growth to these hydrologic variables.

RESULTS

Although baldcypress trees were much longer lived than freshwater mussels resulting in longer growth chronologies, the period of overlap in growth and hydrological data was comparable for baldcypress and mussels (Table 1). The period of overlap ranged from 53–84 years for baldcypress and 17–51 years for mussels from the Sipsey and Little Tallahatchie Rivers. Mussel growth chronologies were shorter in the St. Francis River because the species examined had shorter life spans than the species collected in the other two rivers.

Mean interseries correlations were high for both mussels (0.37–0.96) and baldcypress (0.52–0.67) showing that, within a population, most individuals share a high percentage of non-age related variation in growth (Table 1). Mean interseries correlations were less variable and slightly higher on average for baldcypress (mean across populations = 0.62) than for mussels (mean = 0.55, Mann-Whitney test, $U = 18$, $P = 0.06$) but the range of values overlapped widely among taxa.

Mussel growth in the Sipsey River showed strong, consistent relationships to hydrological variables (Table 3). For each species, growth was significantly correlated to at least one variable. Across species in the Sipsey River, growth was negatively related to variables indicative of high flow conditions (May flows, June flows, high pulse count) and positively related to variables indicative of low flow (low pulse count, low pulse length). Five of nine species were negatively correlated with spring flows (May or June) and high pulse count, and positively correlated with low pulse count. For non-significant correlations with these variables, the signs of coefficients were consistent with significant correlations in all cases except for *Obovaria unicolor* and high pulse

Table 1. Characteristics of growth chronologies of freshwater mussels and baldcypress.

Species	Ecosystem	Growth Time-series	N	Mean Inter-series R	Overlap in Flow Record	Source
Freshwater mussels						
<i>Quadrula pustulosa</i> (Lea, 1831)	Little Tallahatchie River, MS	1966–2003	17	0.52	1966–2003	This study
<i>Elliptio arca</i> (Conrad, 1834)	Sipsey River, AL	1974–2005	21	0.50	1974–2005	This study
<i>E. crassidens</i> (Lamarck, 1819)	Sipsey River, AL	1949–1999	10	0.50	1949–1999	This study
<i>Fusconaia cerina</i> (Conrad, 1838)	Sipsey River, AL	1954–2005	29	0.49	1954–2005	This study
<i>F. ebena</i> (Lea, 1831)	Sipsey River, AL	1955–1999	5	0.37	1955–1999	This study
<i>Lampsilis ornata</i> (Conrad 1835)	Sipsey River, AL	1982–2005	23	0.60	1982–2005	This study
<i>Obovaria unicolor</i> (Lea, 1845)	Sipsey River, AL	1963–1998	8	0.55	1963–1998	This study
<i>Pleurobema decisum</i> (Lea, 1831)	Sipsey River, AL	1955–1999	12	0.37	1955–1999	This study
<i>Quadrula asperata</i> (Lea, 1861)	Sipsey River, AL	1966–2005	26	0.49	1966–2005	This study
<i>Q. verrucosa</i> (Rafinesque, 1820)	Sipsey River, AL	1982–1999	17	0.56	1982–1999	This study
<i>Lampsilis teres</i> (Rafinesque, 1820)	St. Francis River, AR	1993–2002	9	0.76	1993–2002	This study
<i>Potamilus purpuratus</i> (Lamarck, 1819)	St. Francis River, AR	1995–2003	8	0.96	1995–2003	This study
<i>Quadrula quadrula</i> (Rafinesque, 1820)	St. Francis River, AR	1991–2003	5	0.49	1991–2003	This study
Trees						
<i>Taxodium distichum</i> (Linnaeus, 1810)	Altamaha River, GA	929–1985	60	0.60	1932–1985	(Stahle et al. 1996)
<i>T. distichum</i>	Cache River, IL	1468–1985	39	0.61	1923–1985	(Stahle 1996)
<i>T. distichum</i>	Choctawhatchee River, FL	899–1992	111	0.63	1930–1992	(Stahle and Cleaveland 2005a)
<i>T. distichum</i>	Nottoway River, VA	1171–1984	53	0.66	1931–1984	(Stahle and Cleaveland 2005b)
<i>T. distichum</i>	Sipsey River, AL	1852–2006	23	0.52	1929–2006	This study
<i>T. distichum</i>	Ocmulgee River, GA	1202–1984	41	0.66	1900–1984	(Stahle and Cleaveland 1996a)
<i>T. distichum</i>	St. Francis River, AR	1321–1990	81	0.67	1931–1989	(Stahle and Cleaveland 1996b)

count. Correlations of growth with high and low pulse length showed weaker but similar patterns across species in the Sipsey River.

Mussel growth in the St. Francis and Little Tallahatchie Rivers showed less consistent relationships to hydrological variables (Table 3). In the St. Francis River, growth of *Potamilus purpuratus* was negatively correlated to high pulse count but positively correlated to high pulse length; signs of the other two species were consistent with *P. purpuratus* but their correlations were not significant for these two variables. There were no significant

correlations with May or June flows, low pulse count, or low pulse length in the St. Francis River. The strongest and most consistent trend in the St. Francis River was the strong, positive correlations between mussel growth and hydrologic reversals. Mussel growth in the Little Tallahatchie River was not significantly correlated with any hydrologic variable.

Baldcypress growth also showed consistent relationships with hydrological variables but these patterns contrasted oppositely to patterns of mussel growth (Table 3). Baldcypress growth was positively

Table 2. Explanation of hydrologic descriptors used in this study.

Variable	Definition
May flows	Median flow value for the calendar month of May ($\text{m}^3 \cdot \text{s}^{-1}$)
June flows	Median flow value for the calendar month of June ($\text{m}^3 \cdot \text{s}^{-1}$)
Low pulse count	Number of times·year ⁻¹ flow was < 25 th percentile
High pulse count	Number of times·year ⁻¹ flow was > 75 th percentile
Low pulse length	Number of days·year ⁻¹ flow was < 25 th percentile
High pulse length	Number of days·year ⁻¹ flow was > 75 th percentile
Date min.	Julian date of flow minimum for calendar year
Date max.	Julian date of flow maximum for calendar year
Reversals	Number of times·year ⁻¹ hydrograph switched direction (i.e., change from falling to rising river or vice versa)

related to variables indicative of high flow conditions (May or June flows, six of seven populations; high pulse count, three of seven populations) and negatively related to low flow variables (low pulse count, three of seven populations). In addition, signs of non-significant correlations were consistent with these patterns for May and June flows, high pulse count, and high pulse length (positive correlation coefficients), and for low pulse count and low pulse length (negative correlation coefficients). Baldcy-

press growth in the St. Francis River deviated from these patterns most consistently.

DISCUSSION

We found strong, pervasive relationships between hydrological variables and growth of freshwater mussels and baldcypress trees. The nature of these relationships exemplifies the complex dynamics and interconnectedness of bottomland floodplain eco-

Table 3. Pearson correlation coefficients between annual growth of freshwater mussels and baldcypress trees and nine hydrologic variables. Significant correlations ($\alpha < 0.05$) are indicated in bold.

	May Flows	June Flows	Low Pulse Count	High Pulse Count	Low Pulse Length	High Pulse Length	Date Min.	Date Max.	Reversals
Sipsey River mussels									
<i>Elliptio arca</i>	-0.22	-0.38	0.28	-0.66	0.27	0.13	0.30	0.15	0.11
<i>E. crassidens</i>	-0.35	-0.26	0.29	-0.30	0.33	0.09	0.22	-0.23	-0.04
<i>Fusconaia cerina</i>	-0.14	-0.32	0.31	-0.43	0.27	0.13	0.46	-0.19	-0.05
<i>F. ebena</i>	-0.40	-0.23	0.33	-0.20	0.04	-0.12	0.08	-0.21	0.02
<i>Lampsilis ornata</i>	-0.19	-0.41	0.30	-0.59	0.32	0.02	0.28	0.03	0.02
<i>Pleurobema decisum</i>	-0.22	-0.22	0.33	-0.29	0.05	-0.04	0.11	-0.07	0.24
<i>Quadrula asperata</i>	-0.24	-0.42	0.39	-0.34	0.22	0.18	0.25	-0.21	-0.06
<i>Q. (Tritogonia) verrucosa</i>	-0.13	-0.27	0.26	-0.39	0.55	-0.29	0.37	-0.25	-0.06
<i>Obovaria unicolor</i>	-0.30	-0.17	0.60	0.08	-0.22	-0.19	0.23	-0.27	-0.24
St. Francis River mussels									
<i>Lampsilis teres</i>	0.32	0.35	0.29	-0.53	-0.03	0.24	-0.66	-0.39	0.88
<i>Potamilus purpuratus</i>	0.26	0.33	0.27	-0.70	0.29	0.89	0.21	-0.14	0.91
<i>Quadrula quadrula</i>	0.26	0.26	0.26	-0.48	-0.01	0.37	-0.29	-0.36	0.62
L. Tallahatchie mussels									
<i>Quadrula pustulosa</i>	0.05	0.20	0.23	0.11	-0.13	-0.09	0.17	0.04	0.07
Baldcypress chronologies									
Altamaha River, GA	0.44	0.54	-0.09	0.21	-0.14	-0.02	0.26	0.05	-0.14
Cache River, IL	0.15	0.43	-0.13	0.32	-0.26	0.04	0.33	0.01	-0.11
Choctawhatchee River, FL	0.49	0.59	-0.48	0.38	-0.14	0.09	0.14	-0.01	-0.24
Nottoway River, VA	0.60	0.57	-0.34	0.13	-0.08	0.12	0.17	-0.17	0.04
St. Francis River, AR	0.06	0.08	-0.17	-0.08	-0.07	0.25	-0.10	0.24	-0.21
Ocmulgee River, GA	0.44	0.52	-0.32	0.23	-0.11	0.17	-0.25	-0.22	-0.33
Sipsey River, AL	0.65	0.15	-0.11	-0.04	0.02	0.10	0.26	-0.20	0.17

systems. In unregulated streams, years of high growth in mussels and baldcypress, respectively, were associated with opposite ends of the hydrologic spectrum; mussels showed higher growth in low flow conditions whereas baldcypress showed highest growth in high flow conditions. Furthermore, mussel growth in a regulated stream showed no relationship with annual metrics of hydrological variability. This disruption of strong linkages between mussel growth and streamflow observed in unregulated streams demonstrates the profound effects flow regulation has on riverine ecosystems.

High flow conditions can be stressful for freshwater mussels in several ways. In other studies, mussel survival, recruitment, and growth were significantly lower in years having higher average discharge (Villella et al. 2004, Howard and Cuffey 2006, Rypel et al. 2008b). In this study, we observed that low growth was associated with the occurrence of high flows during May and June and the number of high water events in a year. High flow events may reduce mussel growth by increasing energy requirements necessary to maintain position in the substrate. Indeed, the sensitivity of mussels to high flows is demonstrated by their patchy occurrence within flow refuges that protect them from scour and high shear stress (Layzer and Madison 1995, Strayer 1999, Howard and Cuffey 2003). High flow also increases food processing costs because mussels must filter and egest higher quantities of non-digestible, particulate inorganic matter associated with turbid conditions after rainfall events (Norkko et al. 2006). Conversely, high growth in low flow years could be supported by elevated concentrations of microbial biomass and algae that constitutes a large fraction of the diet of adult mussels (Christian et al. 2004).

Despite the sensitivity of mussels to high flows, this component of hydrological variability may be equally important to the long-term maintenance of mussel assemblages. For example, periodic high flows are necessary to maintain high quality mussel habitat by removing accumulations of fine sediments (Howard and Cuffey 2003). For some species, fine sediments may negatively impact growth (Hruska 1992), feeding efficiency (Norkko et al. 2006), and juvenile survival (Vaughn and Taylor 1999). Furthermore, many fish species in lowland streams depend on seasonal flooding for successful reproduction (Kwak 1988, Junk et al. 1989, Slipke et al. 2005, Zeug et al. 2005), ultimately affecting the availability of host fishes for mussels.

The importance of long-term hydrologic variability to baldcypress is even clearer. Positive correlations between baldcypress growth and streamflow

have been shown previously (Young et al. 1993, Young et al. 1995, Keeland and Young 1997, Keeland and Conner 1999), in addition to our study. High flows could benefit baldcypress growth by replenishing nutrients on the floodplain or by reducing competition with tree species intolerant of inundation (Smith 2007). Yet, germination of baldcypress in standing water is poor and successful recruitment occurs predominantly in drought years when seeds fall into non-inundated floodplain soil (Demaree 1932, Keeland and Conner 1999). Long-term maintenance of baldcypress populations is therefore also dependent on a wide range of hydrologic conditions.

Among the non-regulated streams in our study, the most consistent deviations from otherwise pervasive patterns, both for mussels and baldcypress, occurred in the St. Francis River. The lack of consistent correlations between baldcypress growth and hydrological variables was likely due to lasting effects of the 1812 New Madrid earthquake that radically altered microsite environmental characteristics for these trees (Stahle and Cleaveland 1996b). The dissimilarity of mussel growth responses to hydrology compared to the Sipsey River can be explained in at least two ways. First, we were limited to short chronologies in the St. Francis River (mean length of chronology = 9.7 years) because two of our study species were short-lived (*Lampsilis teres*, *Potamilus purpuratus*; maximum age about 15 years) and we found no older individuals of *Quadrula quadrula*. Conversely, our much longer chronologies in the Sipsey River (mean = 37.2 years) resulted in better power to detect associations between growth and hydrological variables. Second, differences in mussel growth responses between these two rivers could reflect a biological response to a gradient of hydrological disturbance not specifically explored in this study.

In contrast to the unregulated Sipsey River, the upper St. Francis watershed is regulated by several dams and the entire watershed is altered by a large number of flood control diversions and drainage canals. Even though the effects of regulation in the upper watershed are largely attenuated at our site, flow diversions in the lower watershed may disrupt relationships between growth and hydrology similar to that which we observed in the impounded and highly regulated Little Tallahatchie River. The only strong, consistent relationship observed between mussel growth and hydrology in the St. Francis River was a positive relationship between growth of all species and the annual number of hydrographic reversals. The number of reversals is a subtle descriptor of streamflow that is difficult to interpret

with regard to its potential effects on mussel growth. The number of reversals could be positively associated with the number of rainfall events sufficient to cause a rise in stream discharge even if these events were not large enough to result in flood pulses. In a highly agricultural landscape such as the St. Francis watershed, even small rainfall events likely transport agricultural fertilizers into the stream, increasing primary productivity and mussel growth. This and other potential relationships between streamflow and mussel growth highlight the need to conduct studies similar to ours across a wide range of landscapes and stream types.

Our results showed complex relationships between hydrology and growth of disparate organisms in bottomland floodplain river ecosystems. Hydrologic conditions in which growth was maximized differed across taxa. Furthermore, even though one integral component of a species' life history (e.g., annual growth rate) may depend on a specific set of hydrologic conditions, another component (e.g., recruitment) may require a completely different range of conditions. These variable responses to pervasive environmental conditions are likely central to the maintenance of biological diversity in floodplain ecosystems. Conservation programs must focus not only on maintaining or recreating natural discharge schedules, but also on preserving the full range of hydrologic variability inherent to these systems.

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